



When a trap is not a trap: converging entry and exit rates and their effect on trap saturation of black sea bass (*Centropristis striata*)

Nathan M. Bacheler*, Zeb H. Schobernd, David J. Berrane, Christina M. Schobernd, Warren A. Mitchell, and Nathan R. Gerdli

Southeast Fisheries Science Center, National Marine Fisheries Service, 101 Pivers Island Road, Beaufort, NC 28516, USA

*Corresponding author: tel: +1 252 838 0825; fax: +1 252 728 8784; e-mail: nate.bacheler@noaa.gov

Bacheler, N. M., Schobernd, Z. H., Berrane, D. J., Schobernd, C. M., Mitchell, W. A., and Gerdli, N. R. When a trap is not a trap: converging entry and exit rates and their effect on trap saturation of black sea bass (*Centropristis striata*) – ICES Journal of Marine Science, doi:10.1093/icesjms/fst062.

Received 12 February 2013; accepted 1 April 2013.

Catch rates are often used to index the abundance of marine organisms, but catch saturation (i.e. declining catch rate as fishing time increases) can decouple catch and abundance. Researchers have struggled to account for saturation when using trap catch to infer population dynamics. We used the underwater video to document entries and exits of black sea bass (*Centropristis striata*) from chevron traps ($n = 26$) to quantify catch saturation. Black sea bass catch varied between 3 and 188 individuals for soak times of ~ 90 min. Overall, 3564 black sea bass entered the traps and 1826 exited; therefore, over half (51%) of black sea bass entering traps exited before traps were retrieved. Black sea bass catch rates were non-linear and asymptotic for most (81%) trap samples, despite short soak times. Moreover, catch saturation occurred at 50 min, when the entry rate declined and the exit rate increased to a point where their confidence intervals overlapped. Several lines of evidence suggest that the level of black sea bass catch once saturation occurred may be positively related to true abundance, but additional research is needed to more fully test this hypothesis.

Keywords: chevron trap, index of abundance, reef fish, saturate, snapper-grouper.

Introduction

Modern fisheries stock assessments rely on sound fishery-dependent (i.e. harvest) and fishery-independent (i.e. survey) data. To be useful, surveys must generate an unbiased estimate of abundance such that catches are proportional to the actual abundance of a species across a landscape (Kimura and Somerton, 2006). However, catch and abundance can become uncoupled if, for instance, catchability (i.e. efficiency of the gear) varies across space, time, habitats, or environmental conditions (Hilborn and Walters, 1992; Pollock *et al.*, 2002; Stoner, 2004). In some situations, it may be possible to standardize the catch rates when environmental conditions across the study area vary temporally or spatially (Maunder and Punt, 2004), but rarely will this result in constant catchability because unidentified and uncontrollable factors will still have a significant influence (MacKenzie *et al.*, 2006).

Catch rates are often assumed to be constant over the amount of time a particular fishing gear is fished (Hamley, 1975). For trawls, this assumption is likely valid because trawl durations tend to be relatively short and there is typically sufficient space in the codend for organisms to accumulate (Ragonese *et al.*, 2001). It is more

tenuous, however, to assume constant catch rates for traps, gillnets, or longlines because soak times can vary from hours to days and the area, volume, or amount of gear is typically much more limited (Rodgveller *et al.*, 2008). A variety of approaches have been used to determine if saturation is occurring, but the most common has been to periodically retrieve the gear, count the enmeshed or trapped animals, and redeploy the gear without removing any individuals from the gear. These studies have documented the presence of saturation over the time-scale of hours (Miller, 1979; Powles and Barans, 1980; Kennelly, 1989) to days (Munro, 1974; Morrissey, 1975; Dalzell and Aini, 1992).

Catch saturation is typically attributed to declining entry rates into traps or gillnets as more individuals are caught and space becomes limited, competition or territoriality increases, or the bait is consumed (Kennedy, 1951; Richards *et al.*, 1983; Olin *et al.*, 2004). However, recent research has focused on the importance of exit rates, especially in the trap gear. For instance, greater than 90% of American lobster (*Homarus americanus*) entering lobster traps exited before the trap was retrieved, likely due to agonistic behavioural interactions in and around traps (Karnofsky and Price,

1989; Jury *et al.*, 2001). Similarly high exit rates have been found for blue crabs (*Callinectes sapidus*; Sturdivant and Clark, 2011), and Cole *et al.* (2004) showed that saturation occurred in two individual traps for blue cod (*Parapercis colias*) when exit rates eventually increased enough to offset entry rates. Determining the exact mechanism causing trap saturation is important because it directly affects whether or not catch reflects actual abundance (Beverton and Holt, 1954).

In this study, we used underwater video to quantify the temporal patterns of entries, exits, and catch for black sea bass (*Centropristis striata*) in a multispecies trap survey on the southeast US continental shelf. Black sea bass are an economically important protogynous species found along the coast of Massachusetts through Florida and in the Gulf of Mexico, USA (Wenner *et al.*, 1986). Black sea bass are a demersal reef fish species that tends to aggregate with conspecifics. In the southeastern United States, the successful assessment and management of black sea bass relies, in part, on reliable fishery-independent survey trap data (SEDAR, 2011). The objectives of our study were to (i) determine if black sea bass catches saturated within soak times typical for the trap survey (i.e. 90 min), and (ii) determine whether saturation occurred due to declining entry rates, increasing exit rates, or both. These results help us understand the catch dynamics of a passive fishing gear and provide clues about why trap catch may saturate.

Methods

Data collection

Sampling for this study occurred in Atlantic Ocean continental shelf waters of the southeastern United States (hereafter, “SEUS”), specifically in waters off Georgia and Florida. Sampling targeted reef fish that typically associate with hard substrates, which occur as scattered patches within the dominant sand and mud substrate in the SEUS (Fautin *et al.*, 2010). Patches of hard substrates in the SEUS are diverse and consist of flat limestone pavement, ledges, rocky outcroppings, or reefs, often colonized by various types of attached biota (Kendall *et al.*, 2008; Schobernd and Sedberry, 2009).

Sampling was conducted by the SouthEast Fishery-Independent Survey (SEFIS), a US National Marine Fisheries Service fishery-independent sampling programme, using a simple random sampling design. Each year, the number of stations is randomly selected from a sampling frame of ~2600 hardbottom stations maintained by SEFIS and the Marine Resources Monitoring, Assessment, and Prediction (MARMAP) programme of the South Carolina Department of Natural Resources. Twenty-three stations included in the analyses below (88%) were randomly selected from the sampling frame, and the remaining three hardbottom stations were newly found and sampled opportunistically. All sampling for this study occurred during daylight hours between April and September 2012 aboard the RV “Savannah” (Table 1).

Chevron fish traps, also known as arrowhead or Madeira traps, were deployed at each station selected for sampling in this study. Fish traps are a versatile gear for reef fish because they (i) can fish unattended, (ii) are suitable for most bottom types and depths, (iii) are inexpensive and robust, and (iv) often catch fish alive so that individuals caught as bycatch can be returned to the water unharmed (Miller, 1990). Fish traps are commonly used around the world to index the abundance of various types of fish and invertebrate species (e.g. Recksiek *et al.*, 1991; Evans and Evans, 1996; Jones *et al.*, 2003; Wells *et al.*, 2008; Rudershausen *et al.*, 2010).

We used chevron fish traps during annual fishery-independent surveys conducted by SEFIS. Chevron traps were constructed from plastic-coated galvanized 12.5 gauge wire (mesh size = 3.4×3.4 cm) and were shaped like an arrowhead measuring $1.7 \text{ m} \times 1.5 \text{ m} \times 0.6 \text{ m}$, with a total volume of 0.91 m^3 (Figure 1). The funnel of each trap was constructed from hexagonal wire mesh ~3.4 cm in diameter, and the mouth opening of each chevron trap was shaped like a teardrop measuring ~18 cm wide and 45 cm long (Figure 1). Each trap was weighted using cylindrical steel rods weighing a total of 11 kg and baited with 24 menhaden (*Brevoortia* spp.; approximate weight of each individual = 180 g), 16 of which were attached to four freely accessible stringers and the other 8 placed loosely inside the trap. A stainless steel cable bridle on the side of each chevron trap was connected to two surface buoys by 8-mm diameter polypropylene lines used for trap retrieval. Usually, chevron fish traps were deployed individually in a group of six traps, with each trap soaking for ~90 min. The minimum distance between individual traps was at least 200 m to provide some measure of independence between traps.

Each trap was deployed with a high-definition video camera (Figure 1). A GoPro Hero® camera was attached to the side of the trap, looking inward towards the mouth opening of the trap, so that reef fish entries and exits could be recorded (Figure 1). Water clarity was always high enough to see the mouth opening and inside of the trap clearly (i.e. ≥ 2 m). Cameras were turned on and set to record before the trap was deployed and recording was stopped when the trap was retrieved, so that video captured the entire time the trap fished.

Video analysis

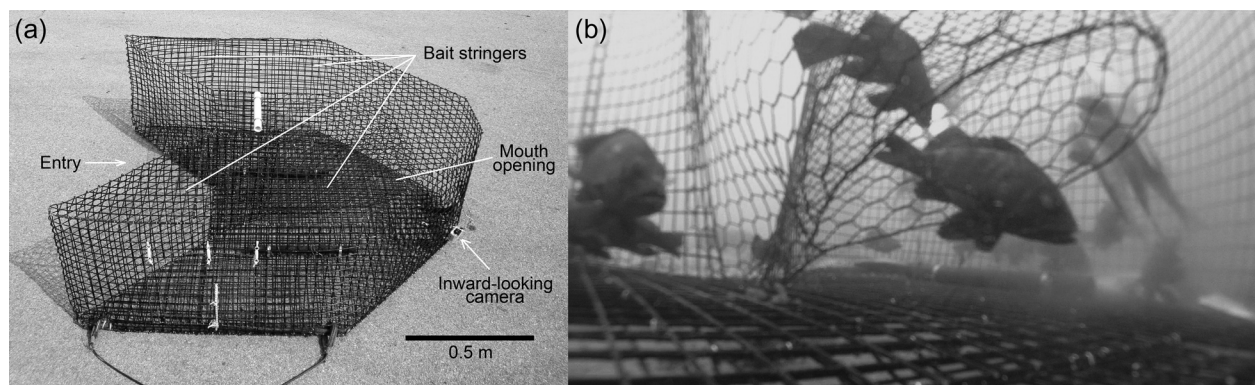
In April 2012, we placed inward-looking GoPro cameras on the first two traps of every trap set. Video data collected from cameras during this cruise suggested that black sea bass were an ideal species upon which to focus this research because they were often caught in large numbers, along with relatively few individuals of other species (e.g. tomtate *Haemulon aurolineatum*, grey triggerfish *Balistes capricus*; Table 2). In the remaining research cruises in 2012, we generally targeted our deployments of inward-looking cameras to stations where we expected to catch black sea bass based on data from previous years. In all, 120 videos of trap deployments documenting entries and exits of reef fish species from chevron fish traps were collected in May–September 2012. Videos were excluded from analysis if they (i) were missing video segments between trap deployment and retrieval or any video files were corrupt, (ii) were too dark at some point during deployment so that fish entries or exits may have been missed, (iii) did not catch any black sea bass, (iv) caught potential black sea bass predators such as gag (*Mycteroperca microlepis*) or red snapper (*Lutjanus campechanus*), or (v) caught a large number of individuals of species other than black sea bass.

For each video included in the analysis, we recorded the time when the trap landed on the bottom, the time when the trap retrieval began, and the time that the trap exited the water. For all analyses, soak time was defined as the time that elapsed between when the trap landed on the bottom (and began fishing) to the time when trap retrieval process commenced (i.e. trap began to lift off the bottom). We only included in our analyses entries and exits occurring until the trap retrieval process began, thus excluding a potentially limited number of entries and exits occurring during trap retrieval.

Table 1. Station-level information for each of the 26 trap video samples included in the analysis of entry and exit rates of black sea bass (*C. striata*) from chevron fish traps.

Trap number	Cruise	Date (2012)	Soak time (min)	Depth (m)	BSB catch	Total entries	Total exits	Exit rate (%)	Other species
1	1	27 April	83	24	69	106	37	35	0
2	1	27 April	85	24	28	43	15	35	3
3	1	27 April	88	23	124	273	149	55	2
4	1	27 April	86	24	88	242	154	64	11
5	1	29 April	80	42	3	4	1	25	2
6	1	30 April	81	52	3	4	1	25	8
7	2	23 May	81	24	89	206	117	57	51
8	2	23 May	84	24	64	168	104	62	0
9	2	25 May	77	37	5	12	7	58	8
10	2	26 May	79	23	18	55	37	67	1
11	2	28 May	82	29	11	14	3	21	1
12	2	29 May	91	27	41	192	151	79	5
13	2	29 May	88	26	85	143	58	41	2
14	3	12 July	85	41	57	73	16	22	10
15	3	12 July	89	42	34	46	12	26	1
16	4	25 August	76	32	24	39	15	38	10
17	4	25 August	82	37	103	144	41	28	64
18	4	27 August	82	20	85	167	82	49	1
19	4	31 August	90	33	71	99	28	28	4
20	5	19 September	81	17	35	114	79	69	8
21	5	19 September	91	18	92	222	130	59	30
22	5	19 September	106	19	164	324	160	49	10
23	5	19 September	99	19	188	361	173	48	33
24	5	19 September	108	19	122	193	71	37	4
25	5	20 September	89	19	3	3	0	0	0
26	5	20 September	88	20	183	270	87	32	16

Soak time was defined as the time that elapsed between when the trap landed on the bottom (and began fishing) to the time when the trap retrieval process commenced (i.e. trap began to lift off the bottom). BSB catch is the number of black sea bass contained in the trap when the trap retrieval process began. Other species is the total number of individuals of all species, not including black sea bass, caught in the trap.

**Figure 1.** (a) Chevron trap fitted with high-definition, inward-looking video camera, which was used to examine the entry and exit rates of black sea bass (*C. striata*) in GA and FL, USA, 2012. (b) Still image from the underwater video camera showing chevron trap mouth opening used to quantify the entry and exit rates of black sea bass (pictured).

The times of each individual entry and exit for black sea bass and all other species were recorded during the entire soak time. To qualify as an entry or exit, an individual fish must have crossed its entire body past the plane of the trap mouth opening (Figure 1). We could not distinguish individuals within a species, so the same individual may have entered and exited the trap multiple times. Sand perch (*Diplectrum formosum*) and bank sea bass (*Centropristis ocyurus*) were excluded from all analyses because they were often small enough to enter and exit through the mesh of the trap. The number of individuals of each species in the trap at any given time during the soak time was calculated as the

cumulative number of entries minus the cumulative number of exits for each minute of soak time.

Data analysis

We were first interested in whether black sea bass catch (i.e. number of fish in the trap when retrieval began) was related to the total number of entries, the total number of exits, or the exit rate of black sea bass in the chevron trap survey. The exit rate was calculated as the per-capita rate of black sea bass exiting the trap once they entered, i.e. the proportion of fish entering that ultimately exited. General linear models were used to test the relationship between

Table 2. Total entries and exits of fish species caught in all 26 chevron traps combined in GA and FL, from the time the trap landed on the bottom and began fishing until the trap retrieval process began.

Common name	Scientific name	Entries	Exits	Per cent caught	Per cent escaped
Black sea bass	<i>Centropristis striata</i>	3564	1826	49	51
Spottail pinfish	<i>Diplodus holbrookii</i>	4	2	50	50
Tomtate	<i>Haemulon aurolineatum</i>	305	140	54	46
Pinfish	<i>Lagodon rhomboides</i>	47	19	60	40
Vermilion snapper	<i>Rhomboplites aurorubens</i>	21	8	62	38
Red porgy	<i>Pagrus pagrus</i>	3	1	67	33
Pigfish	<i>Orthopristis chrysoptera</i>	3	1	67	33
	<i>Stenotomus</i> spp.	47	7	85	15
Grey triggerfish	<i>Balistes capricus</i>	27	2	93	7
Whitespotted soapfish	<i>Rypticus maculatus</i>	2	0	100	0

Bank sea bass (*C. ocyurus*) and sand perch (*D. formosum*) were excluded from analysis because they were commonly seen entering or exiting through the mesh of the trap.

black sea bass catch and total entries, total exits, or exit rate. We used R 2.14.1 (R Development Core Team, 2011) for this and all subsequent analyses.

We next tested for the evidence of trap saturation by examining the relationship between the number of individuals in the trap and the soak time for each trap included in the analysis. We determined the shape of the relationship using a power function of the form (Preston, 1962):

$$y = \alpha x^{\beta}, \quad (1)$$

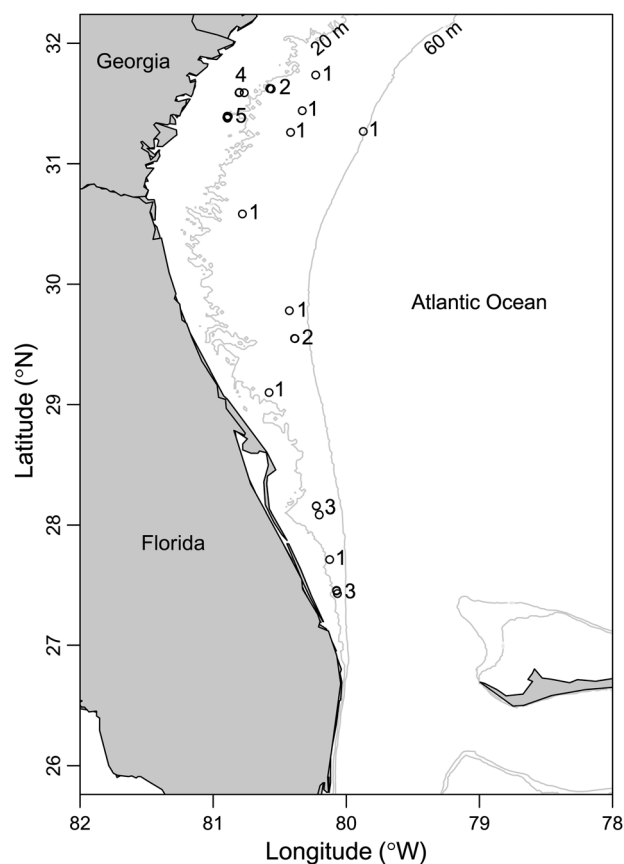
where y is the number of black sea bass in the trap, x is soak time, and α and β are parameters estimated by the model. We were particularly interested in estimates of the constant β . When β was < 1 , then the weight of evidence suggested that the relationship between individuals in the trap and soak time was non-linear and saturating; when β was not significantly smaller than 1, then the evidence did not indicate a non-linear, saturating relationship.

We also determined whether catch rate was invariant across the range of soak times in our study, an assumption that must be met when using catch rate to index abundance. We calculated the number of black sea bass in each individual trap each minute divided by the total soak time of that trap up to that point, and determined the shape of the relationship using a quadratic equation of the form (Zar, 1999):

$$z = ax^2 + bx + c, \quad (2)$$

where z is the mean catch min^{-1} , x is soak time, and a , b , and c are constants. Here, when a was significantly different from zero, there was evidence to suggest that the relationship between catch rate and soak time was non-linear; a significant b value would indicate a slope different from zero.

To determine if saturation resulted from declining entry rates, increasing exit rates, or both, we related the mean number of entries and exits min^{-1} (across all traps) to soak time. We then used quadratic equations (as described above) to determine the form of the relationship between mean entry or exit rate and soak time, with the response variable z here equal to the mean number of entries or exits min^{-1} across all traps. We then plotted the model-based estimates of mean entries and exits min^{-1} , as well as their respective 95% confidence intervals. The soak time at which the confidence intervals first overlapped was considered to be the point at which mean entries and exits were statistically indistinguishable.

**Figure 2.** Map of the study area showing where 26 trap video samples were collected in GA and FL, USA, 2012. The number of trap samples included in the analysis is provided next to each group of open circles; note that symbols overlap. Grey bathymetry lines indicate 20- and 60-m depth contours.

Results

Twenty-six videos of trap deployments documenting black sea bass entries and exits were included in the analysis. These videos were recorded during five research cruises in Georgia and Florida, USA, continental shelf waters between 27 April and 20 September 2012 (Table 1; Figure 2). Depth varied from 17 to 52 m (mean \pm s.d., 27.5 ± 9.3) and soak time ranged from 76 to 108 min (mean \pm s.d., 86.6 ± 7.9).

More black sea bass ($n = 3564$) entered the 26 traps than any other species (Table 2). The number of black sea bass exiting the traps ($n = 1826$) was also considerably greater than any other species. The overall exit rate for black sea bass was 51%, meaning that less than half (i.e. 49%) of the black sea bass entering the traps were eventually caught. The overall black sea bass exit rate was higher than the rate for any other species (which ranged from 0 to 50%), but 7 of 10 species had exit rates greater than 30% (Table 2). Given the high sample sizes for black sea bass but no other species, we limited subsequent analyses to black sea bass only.

The number of black sea bass caught ranged from 3 to 188 individuals (mean \pm s.d., 68.8 ± 54.8 ; Table 1). Between 3 and 361 (mean \pm s.d., 135.3 ± 105.2) black sea bass entered the traps, and between 0 and 173 exited from individual traps (mean \pm s.d., 66.5 ± 58.6). On a trap-specific basis, the black sea bass exit rate for individual traps ranged from 0% (3 entries, 0 exits) to 79% (192 entries, 151 exits; Table 1). There was a positive relationship between total entries and black sea bass catch (linear model: slope \pm s.e. = 1.77 ± 0.15 ; $F_{1,24} = 137.5$; $p < 0.01$; $r^2 = 0.85$), as well as between total exits and black sea bass catch (linear model: slope \pm s.e. = 0.77 ± 0.15 ; $F_{1,24} = 26.1$; $p < 0.01$; $r^2 = 0.50$; Figure 3). However, the exit rate of black sea bass from traps was unrelated to black sea bass catch (linear model: slope \pm s.e. = 0.06 ± 0.07 ; $F_{1,24} = 0.8$; $p = 0.39$; $r^2 = 0.03$; Figure 3). All linear models exhibited constant variance and normally distributed residuals.

The temporal pattern of black sea bass in the trap was non-linear and asymptotic for 21 of the 26 (81%) traps, despite the relatively short soak times of less than 2 h (Table 3; Figure 4). The most drastic example was one trap that caught 99 black sea bass individuals in the first 5 min, but only 84 additional black sea bass in the remaining 84 min. Saturation did not occur for black sea bass in five traps with eventual black sea bass catches of 3, 3, 11, 85, and 103 individuals, as indicated by β values in Equation (1) that were not significantly less than 1 (Table 3). Consequently, the relationship between soak time and overall mean catch min^{-1} of black sea bass was non-linear [Equation (2), $a \pm \text{s.e.} = 0.002 \pm 0.0002$; $p < 0.001$], with catch decreasing as soak time increased ($b \pm \text{s.e.} = -0.03 \pm 0.002$; $p < 0.001$; Figure 5).

The pattern of entries and exits through time was variable among traps (Figure 6). For most traps, entry rates (i.e. the slope of cumulative entries to soak time) were higher earlier than later during the soak time, suggesting a declining entry rate over time. Some traps, however, appeared to have relatively constant entry rates through time. Exit rates were similarly variable, with some increasing, some decreasing, and some remaining constant over time.

When all traps were combined, mean entries min^{-1} declined non-linearly ($a \pm \text{s.e.} = 0.006 \pm 0.003$; $p = 0.04$) from ~ 2 to 1 black sea bass entries min^{-1} , at which point the mean number of entries over time plateaued (Figure 7). Black sea bass mean exits min^{-1} increased non-linearly from 0 to an asymptote around 1 exit min^{-1} ($a \pm \text{s.e.} = -0.002 \pm 0.0003$; $p < 0.01$). The 95% confidence intervals for mean entries and mean exits min^{-1} began overlapping at 50 min, suggesting that mean entries and exits were statistically indistinguishable after a soak time of 50 min.

Discussion

Black sea bass are an economically and ecologically important species in the SEUS, and their successful management depends in

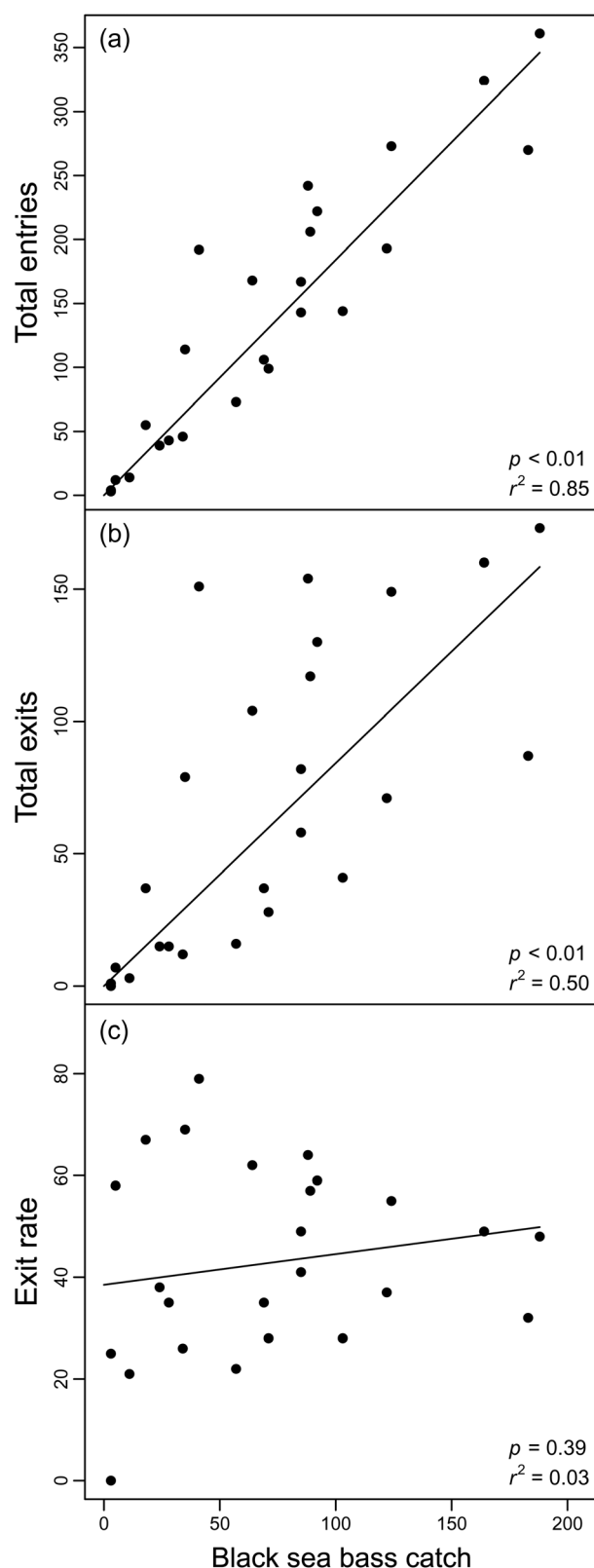


Figure 3. The relationship between total black sea bass (*C. striata*) catch and black sea bass (a) entries, (b) exits, or (c) exit rate (i.e. per cent of all entering black sea bass that exited before trap retrieval).

Table 3. Estimates and s.e. of the β parameter from power model fits to the relationship between black sea bass catch (*C. striata*) and soak time for each of the 26 chevron traps included in the analysis.

Trap number	BSB catch	β	s.e.	p-value
1	69	0.87	0.04	0.001
2	28	0.89	0.03	0.001
3	124	0.44	0.03	<0.001
4	88	0.69	0.06	<0.001
5	3	1.94	0.14	>0.05
6	3	1.27	0.13	>0.05
7	89	0.46	0.01	<0.001
8	64	0.36	0.03	<0.001
9	5	0.18	0.04	<0.001
10	18	0.70	0.06	<0.001
11	11	1.74	0.08	>0.05
12	41	0.13	0.02	<0.001
13	85	0.51	0.02	<0.001
14	57	0.46	0.01	<0.001
15	34	0.83	0.03	<0.001
16	24	0.60	0.03	<0.001
17	103	1.11	0.05	>0.05
18	85	1.38	0.05	>0.05
19	71	0.17	0.01	<0.001
20	35	0.44	0.03	<0.001
21	92	0.49	0.02	<0.001
22	164	0.55	0.03	<0.001
23	188	0.72	0.03	<0.001
24	122	0.91	0.02	<0.001
25	3	0.23	0.02	<0.001
26	183	0.21	0.01	<0.001

BSB catch is the number of black sea bass contained in the trap when the trap retrieval process began.

part on reliable fishery-independent survey trap data (SEDAR, 2011). We found that black sea bass trap catch rates tended to decline over relatively short periods (i.e. <2 h), resulting in catch saturation. Moreover, catch saturation occurred when the declining entry rate converged statistically with an increasing exit rate, after a soak time of 50 min. These results improve our understanding of the dynamics of fish traps and shed light on the mechanisms causing catch saturation, which must be understood to determine whether trap catch is proportional to true abundance (Kimura and Somerton, 2006).

Black sea bass catches in chevron fish traps saturated relatively quickly. In 21 of 26 traps in our study, catch was non-linearly and asymptotically related to soak times of less than 2 h. Theoretically, trap catches will eventually saturate because there is finite space inside a trap that will eventually become filled with animals, which would not permit additional individuals from entering (Bennett, 1974; Austin, 1977; Miller, 1990). Other trap surveys and commercial trap fishers soak traps for much longer periods (e.g. days to weeks), and trap saturation by reef fish has been observed over these longer time frames (Munro *et al.*, 1971; Munro, 1974; Dalzell and Aini, 1992), but there are some notable exceptions. Powles and Barans (1980) used repeated diver counts of fish in traps to show that black sea bass and *Stenotomus* spp. catches saturated in two different types of (non-chevron) fish traps over the course of 3–12 h. Also, trap catches of blue cod were shown to saturate in 30–60 min in New Zealand, but sample sizes were very low ($n = 2$ traps; Cole *et al.*, 2004). Similarly, Bacheler *et al.* (2013a) used long-term chevron trapping data in a regression modelling framework to show that black sea bass catches

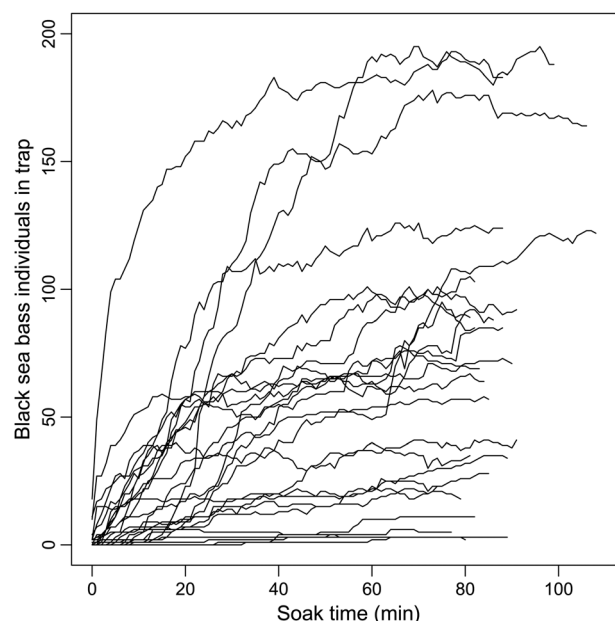


Figure 4. Number of black sea bass (*C. striata*) in each of the 26 chevron trap samples from the time the trap landed on the bottom (time = 0) until the trap retrieval process began (which varied between 76 and 108 min). “Black sea bass individuals in trap” was calculated as the cumulative number of entries minus the cumulative number of exits for each minute of soak time.

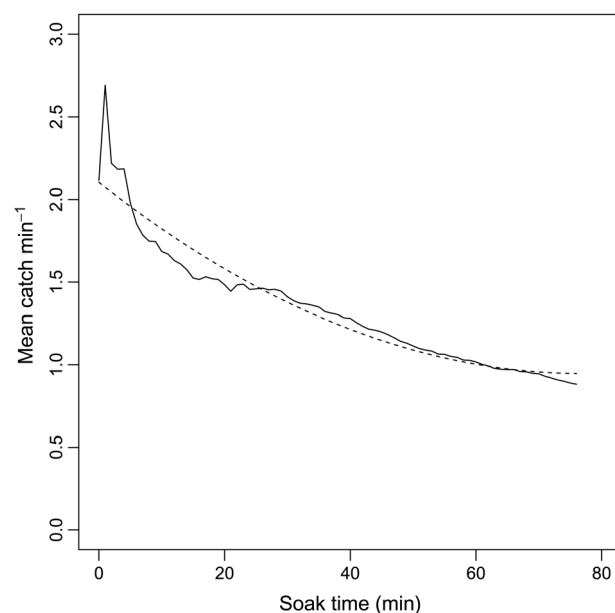


Figure 5. Mean black sea bass (*C. striata*) catch per unit effort (i.e. number of individuals in the trap divided by the soak time; solid line) for all 26 videos collected in GA and FL waters, 2012. Dashed line indicates the quadratic model fit.

were similar regardless of soak times between 50 and 150 min. The fact that black sea bass catch saturated in our study is expected based on theory, but the most noteworthy finding is how quickly the saturation process occurred and, more importantly, why it occurred.

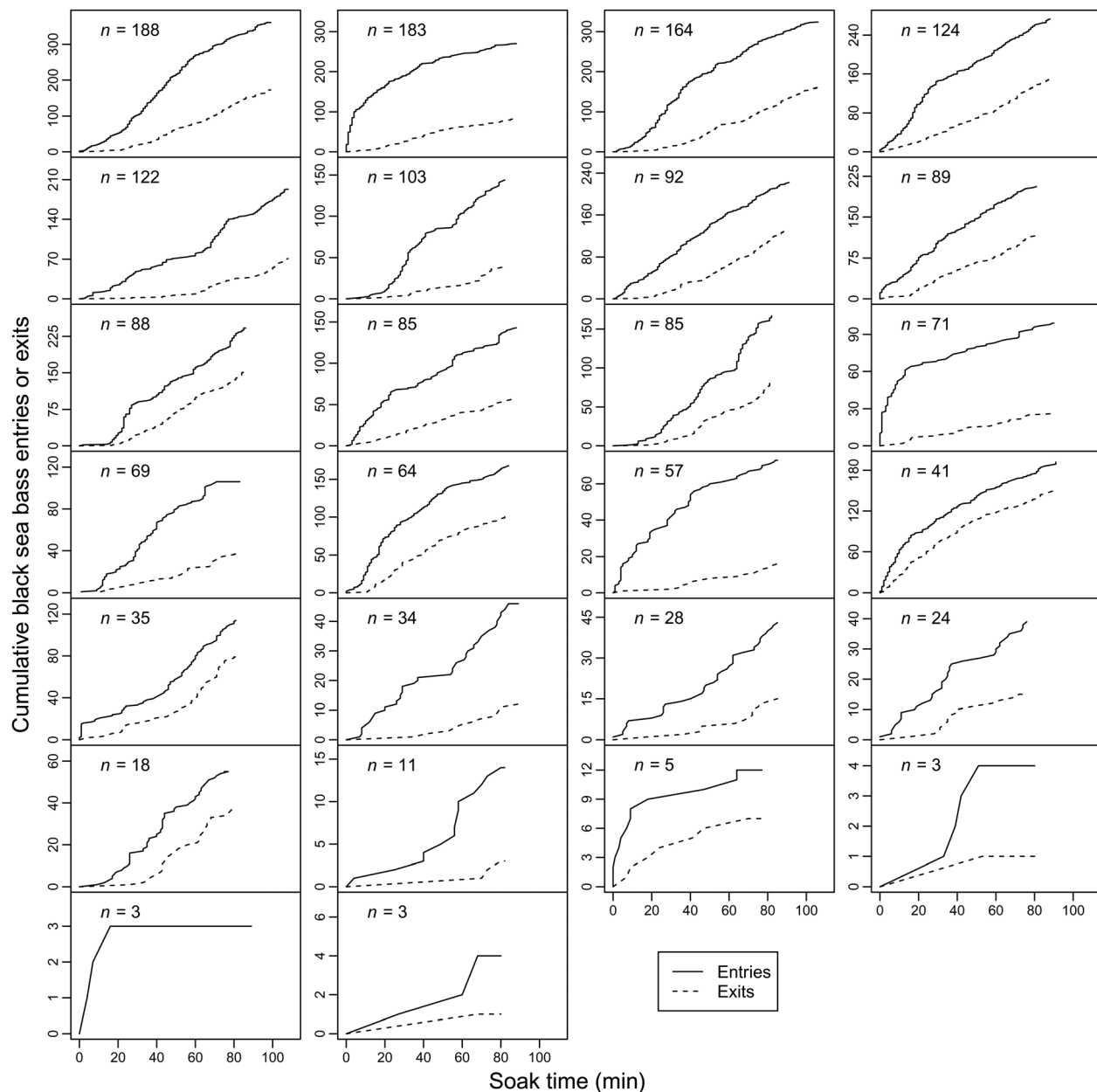


Figure 6. Cumulative number of entries (solid lines) and exits (dashed lines) for black sea bass (*C. striata*) within each of the 26 trap collections included in the analysis. The vertical distance between the two lines represents the number of black sea bass in the trap. Here, traps are plotted in order of descending catch, with the largest catch in the top left panel and the smallest in the bottom right. Note different y-axis scales.

Intraspecific aggressive or territorial behaviours in and around traps is one common explanation for catch saturation, where one or a few dominant individuals defend traps against potential entrants (Jury *et al.*, 2001). However, in those cases, the ultimate level of catch in traps is typically low and saturates at approximately the same level of catch regardless of the variability in actual abundance across a landscape (Addison and Bell, 1997). In our study, black sea bass catch saturated regardless of the magnitude of the catch and no aggressive interactions among black sea bass individuals were observed on video (i.e. similar to Sturdivant and Clark, 2011), suggesting that intraspecific interactions around the trap were not responsible for black sea bass catch saturation. The mean length of black sea bass was also similar among traps in our study,

indicating that size differences were not responsible for the fact that traps saturated at very different levels of catch.

Black sea bass catch did not asymptote due to an entry rate that approached zero, as is commonly assumed, but rather due to a slowly declining entry rate combined with an increasing exit rate. After soak times of 50 min, the entry rate declined and the exit rate increased enough that the two approximately offset each other, resulting in an asymptotic catch. Cole *et al.* (2004) similarly showed that saturation occurred for blue cod when exit rates eventually increased enough to offset entry rates. Our results imply that bait consumption was not responsible for trap saturation because black sea bass were still entering traps regularly (i.e. mean of 1 fish min^{-1}) even when saturation had already occurred, and catch

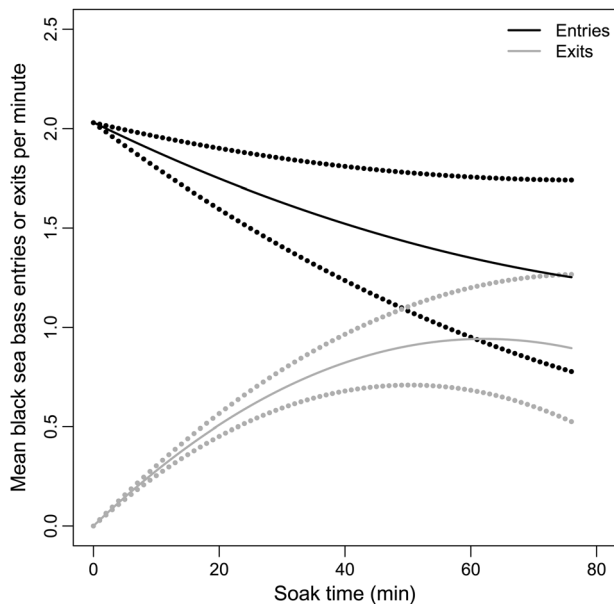


Figure 7. Quadratic model-based mean black sea bass (*C. striata*) entries (solid black line) into, or exits (solid grey line) from, chevron fish traps min^{-1} across all 26 trap collections included in the analysis, 2012. Dotted lines indicate 95% confidence intervals around the entry (black) or exit rate (grey).

rates of reef fish species in unbaited traps may in some instances actually be higher than baited traps (Munro et al., 1971). Regardless, bait was never completely consumed in the traps so fish attraction to the traps was always present, even in traps with the highest catch.

Black sea bass catch, once saturation occurred, is likely positively related to true abundance. In our study, catch of black sea bass inside the trap appeared to be positively related to the number of black sea bass visible on video immediately outside the trap; when catch was large, many black sea bass were simultaneously observed outside the trap, and when catch was low, few black sea bass were observed outside the trap (N. M. Bacheler, pers. obs.). Also, the long-term MARMAP chevron trap index of abundance for black sea bass was highly correlated with many other fishery-independent and fishery-dependent indices in the region (SEDAR, 2011), suggesting that catch was likely proportional to abundance in the trap survey. If black sea bass catch was proportional to abundance, it suggests that chevron traps catch a constant proportion of black sea bass available at each site. More research is clearly required to test the novel hypothesis that black sea bass catch (at saturation) is proportional to true abundance.

Black sea bass catch in five chevron fish traps did not exhibit a statistically significant non-linear, asymptotic relationship. There are two potential reasons for these results. The first explanation is that catch may not have truly saturated, implying that the catch in these traps would continue to increase if soak time increased; if this is the case, longer soak times may be needed in some instances to fully understand the saturation process. Alternatively, determining whether the relationship between catch and soak time is linear or non-linear is likely dependent on the level of catch, and type I error rates are likely higher at low levels of catch (Zar, 1999). In three of the five non-saturating traps, black sea bass catch was low, suggesting that low statistical power may have also contributed to the lack of non-linear fits for these three traps.

Across all traps, 51% of the black sea bass entering traps escaped before the traps were retrieved. The high overall exit rate was much higher than reported elsewhere in the literature for fish (e.g. Cole et al., 2004), with the single exception of Munro et al. (1971), who reported the exit rates of up to 50% for reef fish in the Caribbean but only after much longer soak times (i.e. 14 d). In this regard, our results are more consistent with work on American lobsters, where exit rates were high (i.e. 76–94%; Karnofsky and Price, 1989; Jury et al., 2001). High exit rates may also partially explain why the frequency of occurrence for many reef fish species was higher on video than traps in recent fishery-independent surveys in the SEUS (Bacheler et al., 2013b).

There were three limitations of our approach. First, knowing actual black sea bass abundance around the trap would have allowed a direct comparison between catch at saturation and abundance, but determining actual abundance was not possible in our study. Future studies should attempt to estimate abundance over a broader area around the trap using divers or additional underwater video cameras. Second, stronger inference could have been made if soak times had been longer. We only allowed traps to soak for ~90 min so that our results would directly apply to long-term fishery-independent survey collections in the region. Longer soak times would have allowed us to understand the temporal dynamics of the saturation process more fully, particularly when catch was low (Fogarty and Addison, 1997). Third, we excluded traps that caught potential predators and multiple competitors, so that we could reduce the influence of interspecific interactions on our understanding of the saturation process (Bacheler et al., 2013a). A more complete understanding of the mechanisms causing trap saturation could have been captured had interspecific interactions been explicitly examined.

Gear saturation decouples the often-assumed linear relationship between catch and abundance because catch rates decline until the point when catch stops increasing (Miller, 1990). In some situations, it may be possible to model catch instead of catch per unit effort as the response variable in standardization models and include soak time as a predictor variable in the model (Maunder and Punt, 2004; Bacheler et al., 2013a). But ultimately whether catch or catch per unit effort should be used to index abundance will depend on a clearer understanding of the mechanisms causing gear saturation (Beverton and Holt, 1954). We provided some evidence against some of the more common hypotheses on mechanisms causing trap saturation, such as aggressive behaviours and bait consumption, and suggest that the level of black sea bass catch once saturation occurred may be positively related to true abundance. Clearly, more research is needed to more fully test this hypothesis. Such information will increase our ability to accurately describe population dynamics using fishery-dependent and fishery-independent survey data.

Acknowledgements

We thank the captain and the crew of the RV “Savannah”, staff from the Marine Resources Monitoring, Assessment, and Prediction programme, and many volunteers for making the fieldwork possible. We also thank P. Raley for assisting with camera placement. We benefited greatly from discussions with J. Buckel, L. Coggins, and K. Shertzer, and reviews were provided by M. Burton, A. Chester, A. Hohn, T. Kellison, P. Marraro, and K. Shertzer. The use of trade, product, industry, or firm names, products, software, or models, whether commercially available or not, is for informative purposes only and does not constitute an endorsement by the US

Government or the National Oceanic and Atmospheric Administration.

References

- Addison, J. T., and Bell, M. C. 1997. Simulation modelling of capture processes in trap fisheries for clawed lobsters. *Marine and Freshwater Research*, 48: 1035–1044.
- Austin, C. B. 1977. Incorporating soak time into measurement of fishing effort in trap fisheries. *Fishery Bulletin*, 75: 213–218.
- Bacheler, N. M., Bartolino, V., and Reichert, M. J. M. 2013a. Does reef fish catch saturate with increasing soak time or fish accumulation in a multispecies trap survey? *Fishery Bulletin*.
- Bacheler, N. M., Schobernd, C. M., Schobernd, Z. H., Mitchell, W. A., Berrane, D. J., Kellison, G. T., and Reichert, M. J. M. 2013b. Comparison of trap and underwater video gears for indexing reef fish presence and abundance in the southeast United States. *Fisheries Research*, 143: 81–88.
- Bennett, D. B. 1974. The effects of pot immersion time on catches of crabs, *Cancer pagurus* L. and lobsters, *Homarus gammarus* (L.). *Journal du Conseil International pour l'Exploration de la Mer*, 35: 332–336.
- Beverton, R. J. H., and Holt, S. J. 1954. *On the Dynamics of Exploited Fish Populations*. Chapman and Hall, London. 515 pp.
- Cole, R. G., Alcock, N. K., Tovey, A., and Handley, S. J. 2004. Measuring efficiency and predicting optimal set durations of pots for blue cod *Paraperis colias*. *Fisheries Research*, 67: 163–170.
- Dalzell, P., and Aini, J. W. 1992. The performance of Antillean wire mesh fish traps set on coral reefs in northern Papua New Guinea. *Asian Fisheries Science*, 5: 89–102.
- Evans, C. R., and Evans, A. J. 1996. A practical field technique for the assessment of spiny lobster resources of tropical islands. *Fisheries Research*, 26: 149–169.
- Fautin, D., Dalton, P., Incze, L. S., Leong, J. C., Pautzke, C., Rosenberg, A., Sandifer, P., et al. 2010. An overview of marine biodiversity in United States waters. *PLoS One*, 5: e11914. doi:10.1371/journal.pone.0011914.
- Fogarty, M. J., and Addison, J. T. 1997. Modelling capture processes in individual traps: entry, escapement and soak time. *ICES Journal of Marine Science*, 54: 193–205.
- Hamley, J. M. 1975. Review of gillnet selectivity. *Journal of the Fisheries Research Board of Canada*, 32: 1943–1969.
- Hilborn, R., and Walters, C. J. 1992. *Quantitative Fisheries Stock Assessment: Choice, Dynamics, and Uncertainty*. Springer-Verlag, Berlin. 570 pp.
- Jones, E. G., Tselepidis, A., Bagley, P. M., Collins, M. A., and Priede, I. G. 2003. Bathymetric distribution of some benthic and benthopelagic species attracted to baited cameras and traps in the deep eastern Mediterranean. *Marine Ecology Progress Series*, 251: 75–86.
- Jury, S. H., Howell, H., O'Grady, D. F., and Watson, W. H. 2001. Lobster trap video: *in situ* video surveillance of the behavior of *Homarus americanus* in and around traps. *Marine and Freshwater Research*, 52: 1125–1132.
- Karnofsky, E. B., and Price, H. J. 1989. Behavioural response of the lobster *Homarus americanus* to traps. *Canadian Journal of Fisheries and Aquatic Sciences*, 46: 1625–1632.
- Kendall, M. S., Bauer, L. J., and Jeffrey, C. F. G. 2008. Influence of benthic features and fishing pressure on size and distribution of three exploited reef fishes from the southeastern United States. *Transactions of the American Fisheries Society*, 137: 1134–1146.
- Kennedy, W. 1951. The relationship of fishing effort by gill nets to the interval between lifts. *Journal of the Fisheries Research Board of Canada*, 8: 264–274.
- Kennelly, S. J. 1989. Effects of soak-time and spatial heterogeneity on sampling populations of spanner crabs *Ranina ranina*. *Marine Ecology Progress Series*, 55: 141–147.
- Kimura, D. K., and Somerton, D. A. 2006. Review of statistical aspects of survey sampling for marine fisheries. *Reviews in Fisheries Science*, 14: 245–283.
- MacKenzie, D. I., Nichols, J. D., Royle, J. A., Pollock, K. H., Bailey, L. L., and Hines, J. E. 2006. *Occupancy Estimation and Modeling: Inferring Patterns and Dynamics of Species Occurrence*. Academic Press, Burlington, MA. 344 pp.
- Maunders, M., and Punt, A. 2004. Standardizing catch and effort data: a review of recent approaches. *Fisheries Research*, 70: 141–159.
- Miller, R. J. 1979. Saturation of crab traps: reduced entry and escape-ment. *Journal du Conseil International pour l'Exploration de la Mer*, 38: 338–345.
- Miller, R. J. 1990. Effectiveness of crab and lobster traps. *Canadian Journal of Fisheries and Aquatic Sciences*, 47: 1228–1251.
- Morrissy, N. M. 1975. The influence of sampling intensity on the 'catchability' of marron, *Cherax tenuimanus* (Smith) (Decapoda: Parastacidae). *Australian Journal of Marine and Freshwater Research*, 26: 47–73.
- Munro, J. L. 1974. The mode of operation of Antillean fish traps and the relationships between ingress, escapement, catch and soak. *Journal du Conseil International pour l'Exploration de la Mer*, 35: 337–350.
- Munro, J. L., Reeson, P. H., and Gaut, V. C. 1971. Dynamic factors affecting the performance of the Antillean fish trap. *Proceedings of the Gulf and Caribbean Fisheries Institute*, 23: 184–194.
- Olin, M., Kurkilahti, M., Peitola, P., and Ruuhijärvi, J. 2004. The effects of fish accumulation on the catchability of multimesh gillnet. *Fisheries Research*, 68: 135–147.
- Pollock, K. H., Nichols, J. D., Simons, T. R., Farnsworth, G. L., Bailey, L. L., and Sauer, J. R. 2002. Large scale wildlife monitoring studies: statistical methods for design and analysis. *Environmetrics*, 13: 105–119.
- Powles, H., and Barans, C. A. 1980. Groundfish monitoring in sponge-coral areas off the southeastern United States. *Marine Fisheries Review*, 42: 21–35.
- Preston, F. W. 1962. The canonical distribution of commonness and rarity. *Ecology*, 29: 254–283.
- R Development Core Team. 2011. *R: a Language and Environment for Statistical Computing*. R Foundation for Statistical Computing, Vienna, Austria. www.r-project.org (last accessed 28 March 2013).
- Ragonese, S., Zagra, M., Di Stefano, L., and Bianchini, M. L. 2001. Effect of codend mesh size on the performance of the deep-water bottom trawl used in the red shrimp fishery in the Strait of Sicily (Mediterranean Sea). *Hydrobiologia*, 449: 279–291.
- Recksiek, C. W., Appeldoorn, R. S., and Turingan, R. G. 1991. Studies of fish traps as stock assessment devices on a shallow reef in southwestern Puerto Rico. *Fisheries Research*, 10: 177–197.
- Richards, R. A., Cobb, J. S., and Fogarty, M. J. 1983. Effects of behavioral interactions on the catchability of American lobster, *Homarus americanus*, and two species of *Cancer* crabs. *Fishery Bulletin*, 81: 51–60.
- Rodgveller, C. J., Lunsford, C. R., and Fujioka, J. T. 2008. Evidence of hook competition in longline surveys. *Fishery Bulletin*, 106: 364–374.
- Rudershausen, P. J., Mitchell, W. A., Buckel, J. A., Williams, E. H., and Hazen, E. 2010. Developing a two-step fishery-independent design to estimate the relative abundance of deepwater reef fish: application to a marine protected area off the southeastern United States coast. *Fisheries Research*, 105: 254–260.
- Schobernd, C. M., and Sedberry, G. R. 2009. Shelf-edge and upper-slope reef fish assemblages in the South Atlantic Bight: Habitat characteristics, spatial variation, and reproductive behavior. *Bulletin of Marine Science*, 84: 67–92.
- Southeast Data, Assessment, and Review (SEDAR), 2011. SEDAR 25: stock assessment report for South Atlantic black sea bass. Southeast Data, Assessment, and Review, North Charleston, South Carolina.

- Stoner, A. W. 2004. Effects of environmental variables on fish feeding ecology: implications for the performance of baited fishing gear and stock assessment. *Journal of Fish Biology*, 65: 1445–1471.
- Sturdivant, S. K., and Clark, K. L. 2011. An evaluation of the effects of blue crab (*Callinectes sapidus*) behavior on the efficacy of crab pots as a tool for estimating population abundance. *Fishery Bulletin*, 109: 48–55.
- Wells, R. J. D., Boswell, K. A., Cowan, J. H., and Patterson, W. F. 2008. Size selectivity of sampling gears targeting red snapper in the northern Gulf of Mexico. *Fisheries Research*, 89: 294–299.
- Wenner, C. A., Roumillat, W. A., and Waltz, C. W. 1986. Contributions to the life history of black sea bass, *Centropristis striata*, off the southeastern United States. *Fishery Bulletin*, 84: 723–741.
- Zar, J. H. 1999. *Biostatistical Analysis*, 4th edn. Prentice Hall, Upper Saddle River, NJ. 663 pp.

Handling editor: Shijie Zhou